



Original Articles

Photosynthetic gas-exchange and PSII photochemical acclimation to drought in a native and non-native xerophytic species (*Artemisia ordosica* and *Salix psammophila*)



Ya Juan Wu^{a,b,1}, Cai Ren^{a,b,1}, Yun Tian^b, Tian Shan Zha^{a,b,*}, Peng Liu^{a,b}, Yu Jie Bai^b,
Jing Yong Ma^b, Zong Rui Lai^{a,b}, Charles P.-A. Bourque^{a,c}

^a Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, PR China

^b Key Laboratory of State Forestry Administration on Soil and Water Conservation, Beijing Forestry University, Beijing 100083, PR China

^c Faculty of Forestry and Environmental Management, 28 Dineen Drive, PO Box 4400, University of New Brunswick, New Brunswick E3B5A3, Canada

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ABSTRACT

The mechanisms of plant photosynthetic acclimation to drought remains incomplete. We examined the photosynthetic performance through plant photosystem-fluorescence response to a long-lasting, anomalous summer drought (i.e., lasting for 61 days, with soil water content $< 0.1 \text{ m}^3 \text{ m}^{-3}$) and subsequent post-drought recovery of a native and a non-native desert shrub species (*Artemisia ordosica* and *Salix psammophila*, respectively) growing in northwest China. Key indicators to the examination are derived estimates of plant stomatal conductance (g_s), transpiration (T_r), water use efficiency (WUE), maximum and actual photochemical efficiency (F_v/F_m and Φ_{PSII}), non-photochemical quenching (NPQ), and leaf photosynthesis (P_N) from simultaneous, continuous *in situ* measurements of gas exchange and chlorophyll fluorescence. Chlorophyll fluorescence-associated indicator " F_v/F_m " for both species was down regulated in response to deficits in soil water content (SWC), with differential SWC thresholds of 0.07 and $0.08 \text{ m}^3 \text{ m}^{-3}$ for *A. ordosica* and *S. psammophila*, respectively. The results revealed that both species acclimate to summer drought by a stomatal-regulation mechanism of reducing g_s and WUE and by a PSII NPQ mechanism of dissipating the excessive light energy, indicative of a water-conservation strategy in the acclimation to drought. In comparison with the non-native species, the native species generally had greater photosynthetic performance under water-deficit conditions demonstrating higher transpiration, net CO_2 assimilation, and greater PSII photochemical efficiency. Lower WUE and greater drought resistance and resilience, combined with minor changes in PSII photochemical efficiency are consistent with a well-defined water-conservation response by *A. ordosica*. The results support the hypothesis that native desert-shrub species can potentially outperform non-native shrub species, due to stronger resistance and faster overall recovery from long-lasting drought. Therefore, with increased drought severity and duration anticipated with future climate change, the native shrub species is suggested to be used in desertification control and ecological restoration for sustainable ecosystem management.

1. Introduction

Arid and semi-arid regions make up ~40% of the earth's land surface and are home to ~20% of the human population (Cao, 2008). The severity and duration of summer droughts in arid and semi-arid areas of the world have been increasing, making severe droughts a significant challenge facing dryland ecosystem management both now and in the near future (Schimel, 2010; Piao et al., 2010; Wang et al., 2014). Photosynthesis is particularly sensitive to environmental constraints

(Kalaji et al., 2012). Increasing drought duration may (i) cause photo-inhibition in plants, (ii) promote photo-damage of the photosynthetic apparatus, and/or (iii) lead to the reduction of photosynthetic assimilation (Költhelm et al., 2002; Schurr et al., 2006; Rodríguez-Calcerrada et al., 2008).

Desert plants have evolved a number of adaptive mechanisms in coping with drought-stressed conditions by adjusting their morphological, physiological, and/or biochemical characteristics (Yordanov et al., 2000; Lei et al., 2006; Marcińska et al., 2013; Amisshah et al.,

* Corresponding author at: Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, Beijing 100083, PR China.

E-mail address: tianshanzha@bjfu.edu.cn (T.S. Zha).

¹ Yajuan Wu and Cai Ren contributed equally to this work.

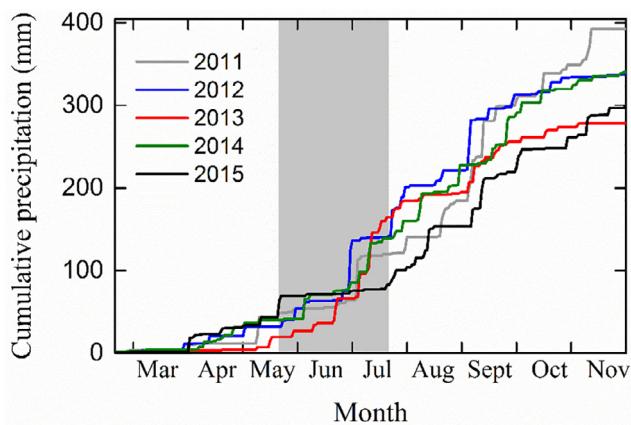


Fig. 1. Annual cumulative precipitation for 2011–2015. The grey band highlights the longest summer period with nominal precipitation among the five years.

2015). Plants in deserts can avoid the effects of droughts by tapping groundwater with deep rooting systems, reducing stomatal opening size and density, promoting waxy surface structures and water-impervious epidermis, and growing small leaves (Brito et al., 2017; Fan et al., 2017). Alongside these morphological changes, desert plants have evolved a variety of physiological and biochemical processes ranging from photosynthetic-related to anti-oxidant defenses (Li and Niyogi, 2001; Allakhverdiev et al., 2008; Doups et al., 2013). For example, non-photochemical quenching (NPQ) is considered as the fastest process employed by plants to relieve the excitation energy pressure in the photosynthetic membrane (location of PSII reaction) and thus protect plants from stressed conditions (Jahns and Holzwarth, 2012; Ruban et al., 2012; Ware et al., 2015). Under conditions of severe and long-lasting drought stress, photosynthesis-related processes, like CO₂ fixation and stomatal conductance (g_s), are maintained by the photosystem I (PSI) cyclic electron transport, when photosystem II (PSII) processes are inactivated (Haldrup et al., 2001; Georgieva et al., 2005; Feng and Cao, 2005; Chaves et al., 2009; Quaas et al., 2015). Inactivation of PSII, induced by water stress, is often attributed to damage to the photosynthetic apparatus, contributing to reversible photo-damage (Yu et al., 2015; Zhang et al., 2016). However, reports addressing the effects of long-lasting water stress on the functioning of PSII are often in dispute.

Recent *in vivo* studies have shown water stress can lead to the damage of PSII reaction centers (Skotnica et al., 2000; Colom and Vazzana, 2003; Campos et al., 2014), whereas other studies have shown that PSII is mostly resistant to water deficits, showing nominal to no change under extreme water shortage (Massacci et al., 2008; Flexas et al., 2009). Overall, mechanisms leading to PSII damage have yet to be fully explored (Georgieva et al., 2005; Sperdouli and Moustakas, 2012). Although prior studies have provided to our understanding of the relationship between photochemical processes and water-deficit conditions in some areas of the world and for specific biomes, our understanding of photochemical responses in desert shrub species and their physiological acclimation to severe water-deficit conditions remains poor.

Prior studies have examined photosynthetic and photochemical response to drought using manipulative experiments performed at fixed times (Sofa et al., 2009; Balachowski et al., 2016; Ashbacher and Cleland, 2016). Such experiments cannot provide detailed understanding of plant physiological acclimation processes that tend to evolve over time. To permit a holistic understanding of drought influences, we need to examine plant responses during and after a drought event (Flexas et al., 2006; Niinemets, 2010; Grant et al., 2014).

Chlorophyll fluorescence (ChlF) is a non-destructive method currently used in the detection of plant photosynthetic performance (Maxwell and Johnson, 2000; Sperdouli and Moustakas, 2012;

Montgomery et al., 2016) and in the investigation of acclimatory and adaptive mechanisms in plants (Bukhov and Carpentier, 2004; Borisovamubarakshina et al., 2015; Rul et al., 2016). Continuous *in situ* monitoring of ChlF provides detailed information on the status and function of photosystem II (PSII; Kalaji et al., 2012), making photosynthetic measurements an important component of plant stress studies. Pulse amplitude modulation (PAM) fluorometry can help with *in situ*, non-destructive monitoring of ChlF of PSII and advance our understanding of acclimation processes in plant species growing in harsh environments (Logan, 2007; Baker, 2008; Durako, 2012; Zha et al., 2017a).

Artemisia ordosica (native shrub species) and *Salix psammophila* (non-native species) are two of the most common shrub species found growing in semi-arid areas of the Mu Us desert land (Wei et al., 2016). *A. ordosica* is a native shrub species distributed mostly on infertile soils (Wu et al., 2015; Lai et al., 2016). *S. psammophila*, in contrast, is a non-native species by large-scale afforestation program in semi-arid area in northwest China to stabilize desert sand dunes, due to its larger size and abundance of horizontally distributed roots (Huang et al., 2001; Xiao et al., 2005; Yang et al., 2008). However, with the preponderance of irrigation wells and increased human activity throughout area, groundwater is often deeper than 10 m from the surface (Jia et al., 2014), making groundwater largely unavailable to most desert plants. In the region, precipitation is normally the only source of water available for plant use. Furthermore, climate-induced drought events are currently becoming more severe and long lasting than ever before and has been predicted to continually increase in this area (Piao et al., 2010). Consequently, the health of plant ecosystems in semi-arid area are challenged by increasing water limitation. Many studies have found that the sustainability of dominant species is at risk because of water scarcity. Photosynthetic response to drought and post-drought conditions can be species specific (Ruehr et al., 2015) and vary with drought severity and duration (Cai et al., 2015). Related to these expected changes, two important questions arise for stakeholder: (1) can the two dominant species photosynthetic acclimate to water deficit? and (2) if they can, can *S. psammophila* (as the non-native species) survive increasing drought? It is therefore hypothesized that native desert-shrub species can potentially outperform non-native shrub species, showing stronger resistance and faster overall recovery from drought.

The aim of this study was to evaluate the resilience of *A. ordosica* and *S. psammophila* to long-lasting drought conditions with the integration of traditional photosynthetic gas exchange measurements and continuous *in-situ* ChlF monitoring. The study addresses the following scientific questions, namely (1) what are the effects of a major summer drought on leaf photosynthesis; (2) what are the mechanisms that lead to leaf photosynthesis recovery from severe drought; and (3) how do *A. ordosica* and *S. psammophila* differ in their physiological acclimation to summer drought?

2. Method

2.1. Study site and experimental design

The measurements come from plants growing on a sand dune at the Yanchi Research Station of Beijing Forest University (37°42'31"N, 107°13'47" E, 1530 m above mean sea level), Ningxia, northwest China. The site is located at the southern edge of the Mu Us desert, characterized by sandy soils with a bulk density of 1.6 g·cm⁻³ in the upper 10 cm of the soil profile. The prevailing climate is temperate arid and semi-arid, where rain is scarce, irregularly distributed, and variable from year to year. The mean annual precipitation is 287 mm, 62% of which falls in summer. This area experiences an annual potential evapotranspiration of about 2024 mm. The mean annual temperature is 8.1 °C. All meteorological summaries are based on meteorological data from the Yanchi County meteorological station and represent 51-year averages (1954–2004). On-site vegetation is the result of 10 years of

land recovery following widespread grazing by free-ranging farm animals, predominantly sheep and goats.

A. ordosica is a slow growing native shrub with short needle-shaped leaves and a main root and abundant lateral roots (Wu et al., 2015). *S. psammophila*, in contrast, is a fast-growing non-native shrub with long narrow leaves and long horizontal lateral roots, as long as 1.5 m (Lai et al., 2016). Roots of the two research shrubs are distributed mainly in the first 50 cm of the soil complex. Phenological observations were made using photographs taken twice each week. Phenophases of the two species include three obvious phases, namely, (1) the leaf-expanding phase (during day of year, DOY, 108–141 and 102–147 for *A. ordosica* and *S. psammophila*, respectively); (2) the leaf-expanded phase (DOY 142–266 and 148–242); and (3) leaf-coloring phase (DOY 260–291 and 230–293; refer to Chen et al., 2015, Ren et al., 2018). On-site species-associated biomass for both species provided in Table 2. Soil water availability depends entirely on precipitation as the water table lies 8–10 m below the ground surface (Jia et al., 2014).

2.2. ChlF measurements

Chlorophyll fluorescence measurements were made *in situ* from May to August of 2015 with a PAM fluorometer (PAM 2000, Walz, Effeltrich, Germany). A sample branch was tied to an aluminum support on which a MONI-head/485 of the fluorometer was attached, so that both the MONI-head and branch could sway together in the wind and sample leaf clumps would not detach from the branch and/or clipper head. Positioning of the head was adjusted manually to minimize shading of the leaves. There were three replicates for each species.

Maximum photochemical efficiency of PSII (F_v/F_m , an indicator of environmental stress), photochemical efficiency of PSII (Φ_{PSII} , a measure of the effective quantum yield of photosynthesis under illumination; Genty et al., 1989), and non-photochemical quenching (NPQ, an index of dissipating excess energy; Losciale et al., 2011) were calculated as follows:

$$F_v/F_m = (F_m - F_0)/F_m, \quad (1)$$

$$\Phi_{PSII} = (F'_m - F')/F'_m, \text{ and} \quad (2)$$

$$NPQ = (F_m - F'_m)/F'_m \quad (3)$$

where F' is the steady-state chlorophyll fluorescence in ambient light and F'_m is the maximum fluorescence in ambient light following a saturating light pulse. Daytime F' and F'_m are used to estimate F_0 and F_m at nighttime (Porcar-Castell et al., 2008).

2.3. Photosynthesis gas exchange measurements

Photosynthesis gas exchange measurements were made simultaneously on fully developed leaves every 10 days during June to July 2015. Five replicate measurements were taken for each species. Measurements of photosynthesis (P_N , $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$, when CO_2 concentrations were about 400 ppm) against calculated intercellular CO_2 concentration (typical A-Ci curves) were derived with an LI-6400XT Portable Photosynthesis System, equipped with an LED light source (Li-Cor Inc., Lincoln, NE, USA). The measurements were conducted at a photosynthetic photon flux density of $1800 \mu\text{mol m}^{-2}\text{s}^{-1}$ and were initiated as soon as leaf temperatures and g_s stabilized. Intrinsic water use efficiency (WUE , $\mu\text{mol} \cdot \text{mmol}^{-1}$) and photosynthetic nitrogen use efficiency (NUE , $\mu\text{mol s}^{-1} \text{g}^{-1}$) were calculated as ratios of P_N ($\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$) to transpiration (T_r , $\text{mmol H}_2\text{O m}^{-2}\text{s}^{-1}$) and P_N to leaf nitrogen concentration (N , g m^{-2}), both expressed per unit leaf area.

2.4. Meteorological measurements

Environmental factors were measured simultaneously. All

meteorological sensors were mounted on a 6-m tall eddy-covariance tower situated near the ChlF-sampling area. Incident photosynthetically active radiation (PAR) was measured using a quantum sensor (PAR-LITE, Kipp & Zonen, The Netherlands). Soil water content (SWC) of five pits were monitored near the tower with five ECH2O-5TE sensors (Decagon Devices, USA) placed around the tower at 30-cm depth in the soil. Rainfall measurements were collected using a tipping bucket rain gauge (TE525WS, Campbell Scientific Inc., USA) set at approximately 50 m from the tower. All micrometeorological variables were measured every 10 s, and then averaged or summed every 30-minutes before being stored on data loggers (CR200X for rainfall, CR3000 for all others, Campbell Scientific Inc., USA).

2.5. Data processing and analysis

Here, long-lasting summer drought days were defined as those days with daily mean SWC $< 0.1 \text{ m}^3 \text{ m}^{-3}$ during the June–August period of the year (Zha et al., 2017b). The drought lasted from May 24th to July 23th, accounting for a total of 61 days. The recovery period was defined as the post-drought period of sufficient rainfall, with a discernible increase in SWC $> 0.1 \text{ m}^3 \text{ m}^{-3}$. The post-drought period lasted from July 24th to July 29th, accounting for 6 days after the drought.

Raw ChlF-data were processed with the batch file feature of the WinControl-3 software. Half-hourly values of $F' < 100$ relative units (r.u.) were considered anomalous and were removed from the dataset. The y-intercept of the linear regression to hourly values of Φ_{PSII} and PAR were used as an indicator of stress (Durako, 2012; Zha et al., 2017a). The regression intercept was calculated with:

$$\Phi_{PSII\text{day}} = \alpha \times \text{PAR} + C \quad (4)$$

where $\Phi_{PSII\text{day}}$ is the daytime Φ_{PSII} (whenever $\text{PAR} \geq 10 \mu\text{mol m}^{-2}\text{s}^{-1}$), α is the regression slope (representing light use efficiency), and C is the y-intercept (estimated value, when $\text{PAR} = 0$), which can serve as an alternative of F_v/F_m and an indicator

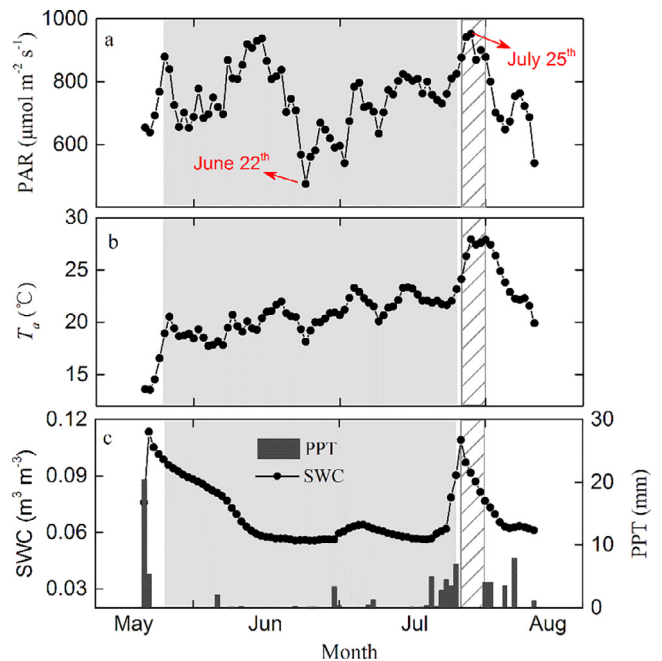


Fig. 2. Variation in incident photosynthetically active radiation (PAR) 6 m above the ground surface (a), air temperature (T_a , b), soil water content (SWC), and precipitation (PPT; c) during the summer drought (May 24th–July 23th, 61 days) and recovery period (July 24th–July 29th, 6 days), respectively. Data values are given as daily means of PAR, SWC, and T_a and daily total PPT. The grey and crosshatched bands represent the longest summer drought and recovery period.

Table 1

Season and annual precipitation from 2011 to 2015, together with the long-term average (1985–2015). Bracketed values are the relative proportion of total annual precipitation.

Year	Precipitation (mm)			
	Spring (Mar–May)	Summer (Jun–Aug)	Autumn (Sep–Nov)	Annual
1985–2015	41 (14.0)	145 (48.6)	106 (36.3)	295
2011	50 (12.5)	146 (36.2)	182 (45.3)	403
2012	52 (15.5)	195 (57.9)	55 (16.4)	337
2013	27 (9.7)	180 (64.6)	72 (25.7)	278
2014	40 (11.6)	186 (54.4)	113 (33.1)	342
2015	68 (22.3)	87 (28.6)	148 (48.6)	302

of stress in a plant species (Durako, 2012; Zha et al., 2017a).

Daily means were computed as the average of hourly means. Daily mean values were used to examine the variation in ChlF-related parameters (F_v/F_m , Φ_{PSII} , NPQ, and y-intercept) and response to changes in SWC (Figs. 4 and 5). Resistance (resilience) to drought was expressed as ratios of the values of P_N , g_s , T_r , WUE, and NUE at the end of the drought (beginning of the recovery period) to those at the beginning (Tilman and Downing, 1994; Darychuk et al., 2012; Lei et al., 2015). Ratios close to 1.0 imply a greater resistance to drought and capacity to recover. We performed independent sample t-tests at a 0.05 significant level to examine the differences between the beginning and end of the drought period (May 24th and July 14th, respectively) and performance difference between species.

3. Result

3.1. Variation in environmental factors

The study site had less precipitation in the summer of 2015 compared with the mean of the past 30 years (1985–2015, Table 1). The precipitation in the summer (June–August period) of 2015 was 87 mm (Bold line in Table 1), accounting for 29% of the annual total, as compared to a summer fraction of 49% for the 30-year average (Table 1). Year 2015 was dry, particularly in summer with a 61-day drought from May 24th to July 23th (Figs. 1 and 2). Daily mean PAR during the drought period ranged from $474 \mu\text{mol m}^{-2} \text{s}^{-1}$ (June 22th) to $951 \mu\text{mol m}^{-2} \text{s}^{-1}$ (July 25th; Fig. 2a). Daily mean T_a ranged from 14°C (May 21th) to 27°C (July 25th; Fig. 2b). There was one precipitation event with $> 20 \text{ mm day}^{-1}$ before the summer (Fig. 2c). Daily mean SWC decreased from $0.12 \text{ m}^3 \text{m}^{-3}$ at the beginning of the summer drought to $0.055 \text{ m}^3 \text{m}^{-3}$ at the end (Fig. 2c). The recovery period was from July 24th to July 29th (6 days), defined by post-drought rainfall, with a clear increase in SWC (Fig. 2c).

3.2. The response of the photosynthetic parameters to summer drought

Fig. 3 provides mean trends in the photosynthetic parameters for *S. psammophila* and *A. ordosica* during the summer drought. All photosynthetic parameters exhibited a declining trend from the beginning to

Table 2

Characteristics of individual plant for *S. psammophila* and *A. ordosica*. Bracketed values are standard error of estimate (SE, $n = 3$).

Characteristics	Species	
	<i>Spsammophila</i>	<i>A-ordosica</i>
Height (m)	2.72 (0.29)	0.50 (0.07)
Canopy coverage (%)	95	80
Aboveground biomass (g m^{-2})	3271 (120)	408 (12)
Root (g m^{-2})	2363 (109)	303 (44)

the end of the drought period, with a percentage drop of 88%, 83%, 84%, 32% and 89% for *S. psammophila* ($p < 0.05$; Fig. 3a–e) and a drop of 54%, 47%, 27%, 25% and 53% for *A. ordosica* ($p < 0.05$; Fig. 3f–j). The decreases were greatest for *S. psammophila* than for *A. ordosica* (Fig. 3), with an exception in WUE, which revealed an opposite trend (Fig. 3d and i). No significant difference was observed in drought resistance between the two shrub species in either g_s and WUE (Fig. 3l and n; $p > 0.05$). During post-drought, resilience associated with the differential response in photosynthetic parameters was greatest in *A. ordosica* than in *S. psammophila* (Fig. 3p–t).

3.3. The response of the photochemical parameters to summer drought

During drought exposure (Figs. 2 and 4), F_v/F_m in *S. psammophila* decreased from an optimal value of ~ 0.73 on July 18th to 0.32 on July 20th, resulting in a 56% decline (Fig. 4a). Similarly, Φ_{PSII} dropped to 0.22 on July 19th from 0.68 on June 3rd, giving a 68% decline (Fig. 4b). The y-intercept of diurnal Φ_{PSII} -to-PAR regressions decreased from 0.71 on July 19th to 0.48 on July 19th (Fig. 4d). In contrast, the value of NPQ increased from 0.71 on May 20th to 3.4 on June 18th (Fig. 4c). Stress indicators (i.e., F_v/F_m , Φ_{PSII} , and the y-intercept of the diurnal Φ_{PSII} -to-PAR regression) recovered to pre-drought values in just three days after the drought (Figs. 2 and 4).

In comparison, the effect of summer drought on *A. ordosica* (Fig. 4e–h) produced a smaller reduction in Φ_{PSII} and F_v/F_m . The F_v/F_m -value decreased from 0.82 on May 27th to 0.63 on July 18th, yielding a 23% decline (Fig. 4e), and the daytime daily mean Φ_{PSII} decreased from 0.68 on May 27th to 0.43 on July 3rd (a 37% drop; Fig. 4f). The value of NPQ increased slowly from 0.38 on June 2nd to 2.4 on August 2nd (Fig. 4g). The y-intercept of the diurnal Φ_{PSII} -to-PAR regression [i.e., C in Eq. (4)] fluctuated gradually over the drought period (Fig. 4h). Values of F_v/F_m and Φ_{PSII} recovered to pre-drought conditions in just two days after the drought (Fig. 4e and f).

Fig. 5 gives the relationship between ChlF-associated parameters as a function of summer SWC. For *S. psammophila*, ChlF-associated parameters F_v/F_m , Φ_{PSII} , and y-intercept of the diurnal Φ_{PSII} -to-PAR regression were limited by SWC, when $\text{SWC} < 0.08 \text{ m}^3 \text{m}^{-3}$ ($p < 0.05$). For *A. ordosica*, however, only F_v/F_m was limited by SWC, when SWC fell below $0.07 \text{ m}^3 \text{m}^{-3}$ ($p < 0.05$).

4. Discussion

4.1. Photosynthetic responses to drought

Summer drought reduced soil water content (SWC) and caused a gradual decline in photosynthetic rate (P_N), stomatal conductance (g_s), transpiration (T_r), and water use efficiency (WUE) in both species (Fig. 3). The decline in P_N was mainly due to stomatal limitation, as it decreased in combination with a decrease in g_s . A notable decrease in g_s in the two species under summer drought suggests an efficient adaptive transpiration control, with the magnitude of control differing between the two species (Fig. 3). This result is in agreement with the diurnal patterns of g_s -response in seedlings during water-deficit conditions, which significantly decreased g_s in the two species (Xiao, 2001). Drought constrained P_N more than T_r in both species (88% and 54% vs. 84% and 27%), causing WUE to be lessened (Fig. 3d and i). These reductions suggest that both species used a water-conservation strategy in responding to soil water deficits (Liu et al., 2007; Zha et al., 2017a). Many woody species acclimate to water deficits through the conservation of water (Reichstein et al., 2007; Li et al., 2009; Cocozza et al., 2010; Wang et al., 2016). Reduction in NUE in both species also indicated a lowering of photosynthetic activity during the drought (Fig. 3e and j; Gebauer and Ehleringer, 2000).

A notable difference in photosynthetic capacity between the two species in response to drought was indicated by differential changes in photosynthetic parameters (Fig. 3), with a greater reduction in *S.*

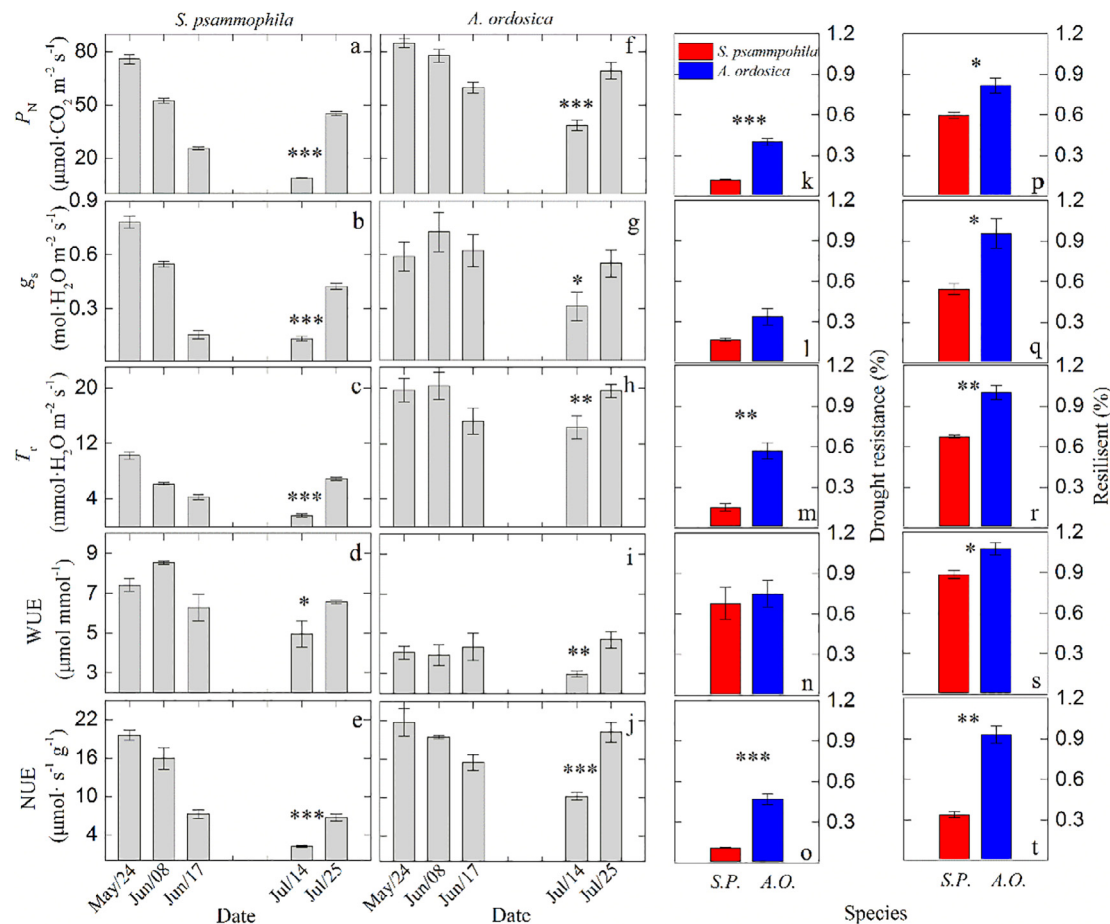


Fig. 3. The effect of summer drought on P_N (leaf photosynthesis; a and f), g_s (stomatal conductance; b and g), E (transpiration; c and h), WUE (water use efficiency; d and i), and NUE (nitrogen use efficiency; e and j) in *Artemisia ordosica* and *Salix psammophila*, respectively. Drought resistance and resilience of *Salix psammophila* (k–o) and *Artemisia ordosica* (p–t) are expressed as ratios of P_N , g_s , E , WUE, and NUE at the end and beginning of the drought and recovery period. The error bars stand for \pm of the first standard error of estimate (SE). The stars over the grey bars indicate significant difference between the beginning (May 24th) and the end of the drought period (Jul 14th); stars over the red and blue bars indicate significant difference in resistance and resilience between the two species, with *, standing for $p < 0.05$; **, for $p < 0.01$; and ***, for $p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

psammophila than in *A. ordosica*, suggesting a lower resistance to drought in *S. psammophila* (Fig. 3k–o). A higher WUE observed for *S. psammophila* was consistent with the fast-growing nature of the species. Fast-growing woody plants normally have a higher WUE under moderately dry conditions, leading to further stress during severe drought (Darychuk et al., 2012; Chen and Zhao, 2015). Native *A. ordosica* used a stronger water conservation strategy, while maintaining stronger photosynthetic capacity and acclimation than was observed in *S. psammophila* during the drought. This result is further supported by the fact that *A. ordosica* demonstrates greater resistance and resilience to drought (Fig. 3). Existing researches support the result that native species appear to have a competitive advantage over non-native species in low-resource environments, where the physiological traits of the species are largely associated with resource conservation (Chapin, 1980; Craine, 2009; Funk, 2013).

The result that *A. ordosica* had a higher photosynthetic rate than *S. psammophila*, does not contradict that the latter species had greater biomass production, as presented in Table 2. The greater biomass production of the latter species is due to its greater leaf area and leaf area index, combined with a greater WUE (Table 2; Fig. 3d and i), which make it greater total leaf area for photosynthesis and thus greater biomass production.

4.2. PSII photochemical responses to drought

Changes in F_v/F_m -values have indicated either down regulation or recovery of the photosynthetic apparatus (Porcar-Castell et al., 2008), which can be caused by adjustments in (i) photochemical capacity, (ii) capacity of the thermal dissipation in PSII, or (iii) both. In most healthy, non-stressed plants, F_v/F_m ranges between 0.73 and 0.81 (Murchie and Lawson, 2013; Zha et al., 2017a). When plants are stressed, the values drop below the 0.73–0.81 range (Verhoeven et al., 1999; Lin et al., 2007). In our study, F_v/F_m reduced at the end of the drought period for both species and recovered soon afterwards with an increase in soil water following a rainfall event (Fig. 3). A reduction in F_v/F_m and an increased in NPQ in response to stress are considered reliable indicators of photo-inhibition and protection activated against stress (Nainanayake, 2007; Mantoan et al., 2015). The acclimation of F_v/F_m over time for plants under long-lasting summer drought and post-drought recovery conditions possibly indicates that the PSII is protected by a mechanism that dissipates excess energy (i.e., NPQ) to prevent the photosynthetic apparatus from becoming damaged (Janka et al., 2015). Increased NPQ enhances excessive energy release through thermal dissipation by plants, circumventing oxidative damage (Li and Niyogi, 2001). This process inhibits the formation of reactive oxygen species that would result from O_2 photo-reduction by way of the Mehler reaction and singlet oxygen formation within the light-collecting

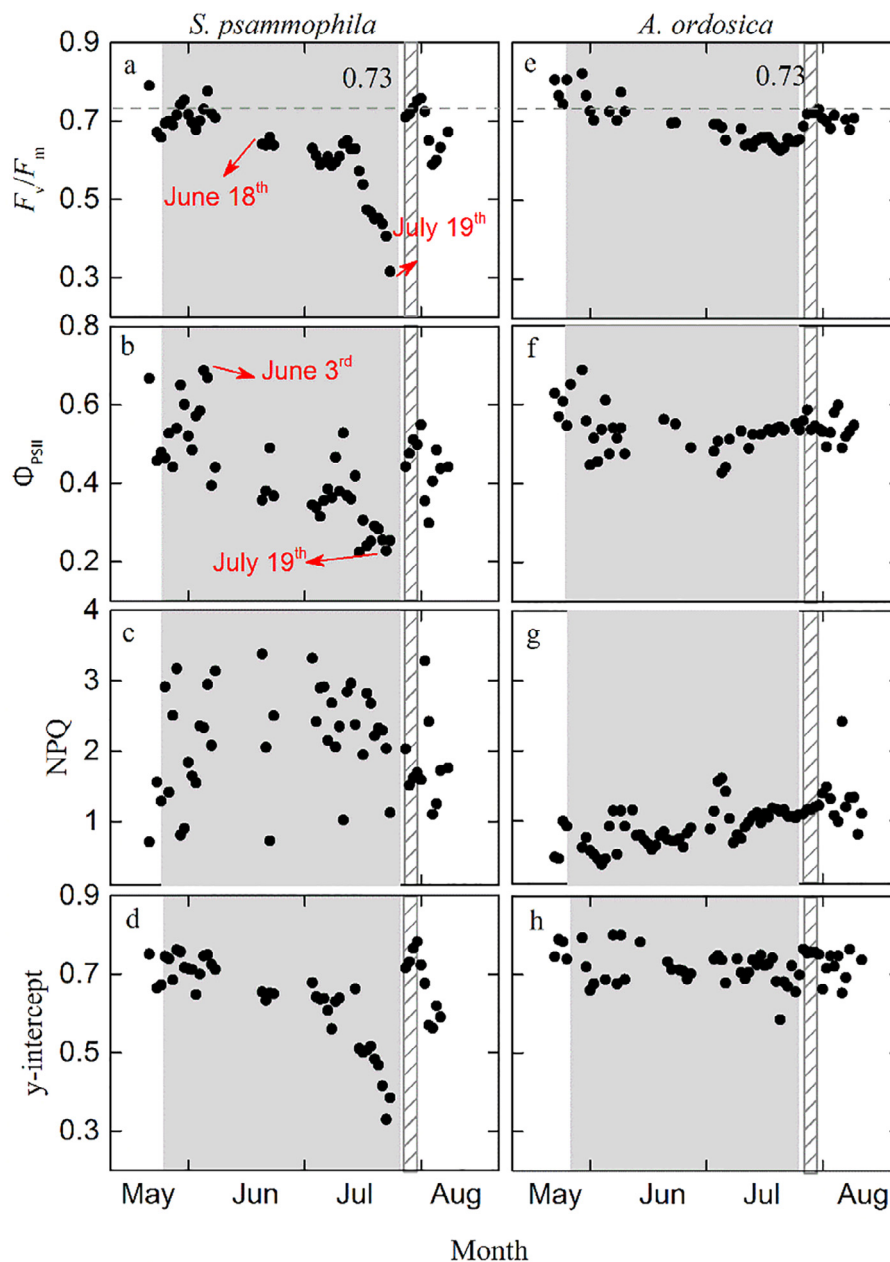


Fig. 4. Variation in daily maximal quantum yield of PSII photochemistry (F_v/F_m ; a and e), daily means of effective quantum yield of PSII photochemistry (Φ_{PSII} ; b and f), daily means of non-photochemical quenching (NPQ; c and g), y-intercept (C, unitless; d and h) of the Φ_{PSII} -to-PAR regression for the two shrub species (*A. ordosica* and *S. psammophila*) during the summer drought. The grey and crosshatched bands give the longest summer drought period (May 24th–July 23th, 61 days) and recovery period (July 24th–July 29th, 6 days), respectively. The broken horizontal lines in panels (a) and (e) mark the F_v/F_m -value of 0.73.

complexes (Hallik et al., 2012). The different thresholds of SWC with changes in the y-intercept of the diurnal Φ_{PSII} -to-PAR regression were consistent, given the fact that *A. ordosica* is a drought-adapted plant with a strong predisposition to PSII photochemical-acclimation to summer drought (Zha et al., 2017a).

Some studies have shown that water stress reduced plant F_v/F_m (Gao et al., 2014; Vineeth et al., 2016). Drought-induced reductions in the two species differed. In *S. psammophila*, we found F_v/F_m to decrease whenever $SWC < 0.08 \text{ m}^3 \text{ m}^{-3}$ and $< 0.07 \text{ m}^3 \text{ m}^{-3}$ in *A. ordosica* (Fig. 5). A smaller SWC threshold suggests that *A. ordosica* is more resistant to drought. *A. ordosica* maintained simultaneously higher photochemical activity, indicated by higher F_v/F_m , Φ_{PSII} , stomata conductance, active transpiration, and net CO_2 assimilation rates, in response to drought than did *S. psammophila* (Figs. 3 and 4). Reduction in photochemical parameters F_v/F_m , Φ_{PSII} , and the y-intercept of the

diurnal Φ_{PSII} -to-PAR regression for both species coincided with photo-inhibition (Fig. 4). Smaller reductions and quick recovery in these parameters for *A. ordosica* indicated that the species was less disturbed by drought. These results are consistent with previous results for desert woody plant species (e.g., Jiang and Zhu, 2001; Chaves and Oliveira, 2004; Spirdouli and Moustakas, 2012; Zha et al., 2017b). These results are, however, in contrast to results from previous studies attending to the difficulty in establishing native plant species on abandoned desert farmland due to the lack of adequate soil moisture (Banerjee et al., 2006). Our results support the hypothesis that native desert-shrub species adapted to a region can potentially outperform non-native shrub species introduced to the region, showing stronger resistance and faster overall recovery from drought.

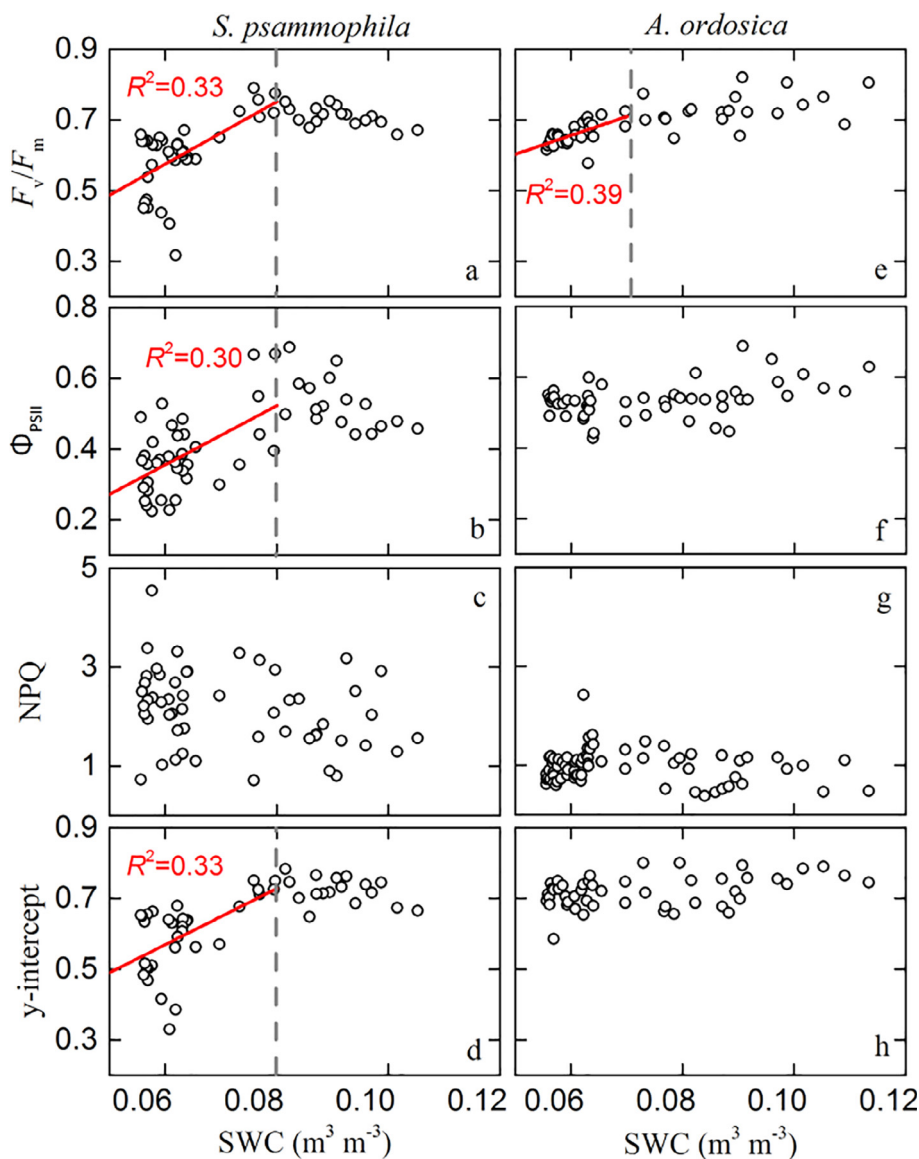


Fig. 5. Response in maximal quantum yield of PSII photochemistry (F_v/F_m ; a and e), effective quantum yield of PSII photochemistry (Φ_{PSII} ; b and f), non-photochemical quenching (NPQ; c and g), and y-intercept of the Φ_{PSII} -to-PAR regressions (C, unitless; d and h) as a function of summer soil water content (SWC) for the two species. The broken vertical line gives the SWC threshold for *S. psammophila* (i.e., $0.08 \text{ m}^3 \text{ m}^{-3}$) and *A. ordosica* ($0.07 \text{ m}^3 \text{ m}^{-3}$), respectively. The red lines are regression fits to the data during the drought period, with $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusion

The photosynthetic capacity was reduced in response to drought with $\text{SWC} < 0.07$ and $0.08 \text{ m}^3 \text{ m}^{-3}$ in two common desert shrub species, *A. ordosica* and *S. psammophila*, respectively. Both species exhibited photo-inhibition, but avoided permanent damage. The two species were shown to acclimate to long-lasting summer drought by reducing stomatal conductance and heat dissipation by non-photochemical quenching mechanism. The native species, *A. ordosica*, was shown to be more resistant and resilient to drought than the non-native species, *S. psammophila*. Both species exhibited a water-conservation strategy in coping with drought, with *A. ordosica* providing stronger water conservation than *S. psammophila*. With continuously increasing drought severity and duration and associated lowering of groundwater anticipated with future climate change, native species *A. ordosica* can be suggested for afforestation and/or reforestation in desertification control and ecological restoration for sustainable ecosystem management.

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